PROC. ENTOMOL. SOC. WASH.
92(1), 1990, pp. 93–97

CUBITUS POSTERIOR IN HYMENOPTERA

W. R. M. Mason

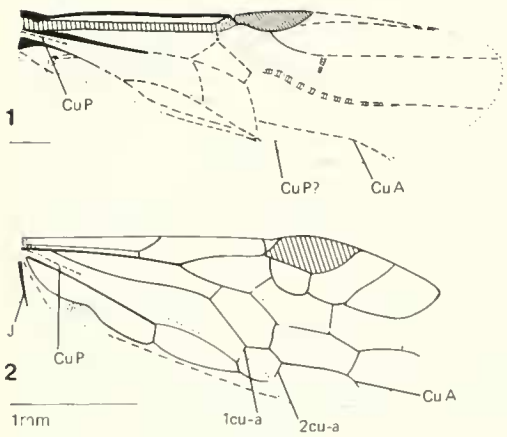
Biosystematics Research Centre, Agriculture Canada, Research Branch, Central Experimental Farm, Ottawa, Ontario K1A 0C6, Canada.

Abstract.—Forewing veins of Hymenoptera named by Ross (1936) Cu, Cu 1, Cu 1a are really Cu A. Ross's vein Cu 1b is a crossvein, 2cu-a, necessitating that Ross's cu-a be called 1cu-a. The rarely seen vein Cu 2 (Ross 1936) in Hymenoptera should be called Cu P. An apparent distal section of Cu P is readily seen in Rhopalosomatidae, and can be seen in spectral form in many other Apocrita.

Key Words: Hymenoptera, venation, wing, Cubitus Posterior, Comstock-Ross system

When Comstock (1895) published his system for naming the veins of Hymenoptera his nomenclature rested on the phylogenetically unsound practice of interpreting the venation of Hymenoptera by comparison with that of higher Diptera (Comstock 1918, p. 383 ff). The serious flaws in the resulting scheme may well have accounted for the general reluctance of hymenopterists of the early 20th century to use Comstock's system (Rohwer and Gahan 1916). These flaws were not corrected until 40 years later when H. H. Ross (Ross 1936) reinterpreted hymenopterous venation by comparing venation of primitive Hymenoptera (Symphyta) with what he then believed to be the most closely related extant orders, Megaloptera, Trichoptera, and Mecoptera. The soundness and brilliance of his interpretation can be seen by the widespread acceptance, with no essential modification, of the Ross system today, over 50 years later.

There were some points about which Ross expressed doubt. One was the identity of the branches of Media and Cubitus. He was familiar with Lameere's and Martynov's system of naming convex veins "anterior" and concave ones "posterior" because he cited Martynov's work and labels veins of many of the non-hymenopterous wings as MA and MP. He decided to call the single Media vein of Hymenoptera "M" mainly for lack of evidence and for convenience. For branches of Cubitus he considered the evidence equivocal, apparently because the posterior branch of the Cubital vein of *Sialis* is neutral in profile, even though falling near the claval furrow in a concave part of the wing. As a compromise he retained the Comstock names for the branches of Cubitus, Cu 1 and Cu 2, the former subdivided into Cu 1a and Cu 1b. Subsequent research has clarified the doubts felt by Ross so that one can no longer justify using Comstock-Ross nomenclature for the branches of Cubitus in Hymenoptera (Carpenter 1966, Wootton 1979, Rasnitsyn 1980). The Lameere hypothesis and its background is best summarized by Carpenter (1966). Comstock's hypothesis is criticized by Lameere and by Martynov (op. cit.). Veins Cu 1 and Cu 2 of the Ross system should be called Cu A and Cu P, respectively, to align hymenopterous vein nomenclature with modern usage and opinion among students of other orders, and especially with usage in



Figs. 1, 2. Symphyta forewings. 1, *Orussus occidentalis* Cr. (Orussidae) to show basal, concave nebular section of Cu P and possible apical, spectral section of Cu P (weakly defined and often absent). 2, *Xyela bakeri* Konow (Xyelidae) to show nebular basal section of Cu P, claval furrow and cu-a crossvein. (Conventions of delineation follow Mason (1986). Scale lines = 1 mm).

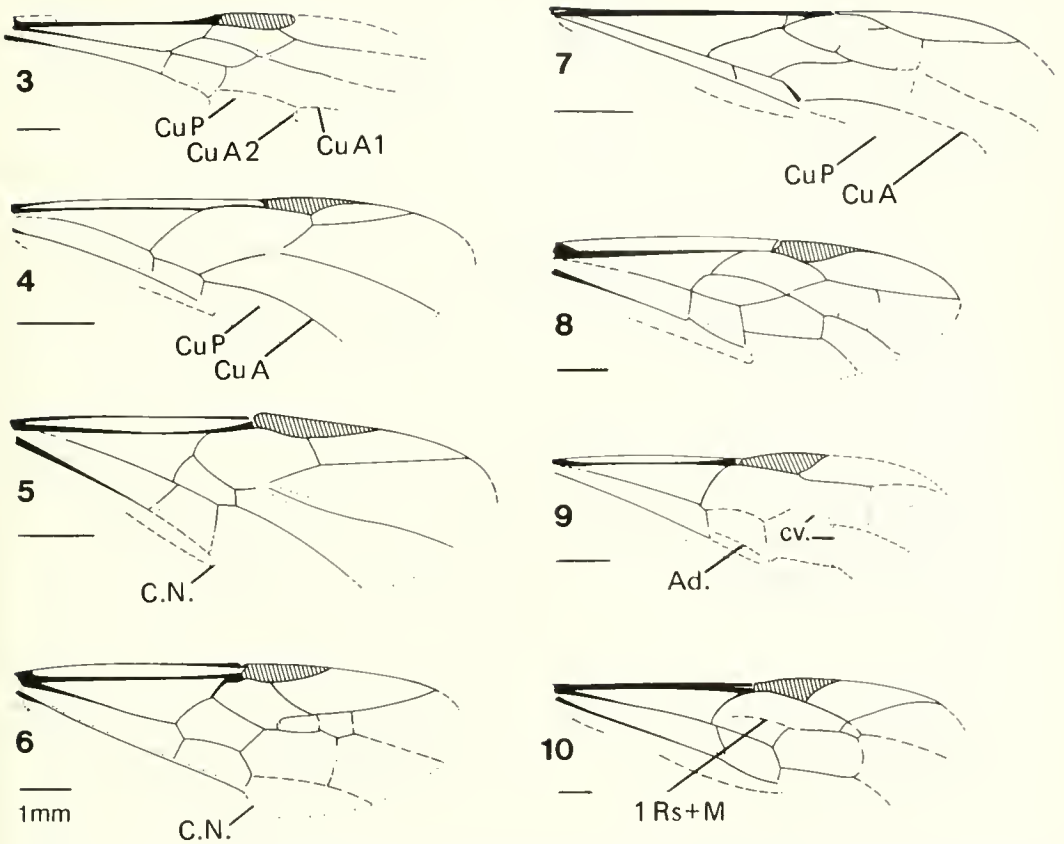
the study of those fossil groups most probably including the sister group of Hymenoptera (Rasnitsyn 1980).

Ross, following Comstock's system, named the two branches of his first cubital vein Cu 1a and Cu 1b. In his figures of non-hymenopterous wings (Ross 1936, figs. 2, 6, 8, 20–22, 24) he shows both Cu 1a and Cu 1b extending to the wing margin far distad of the claval notch (which is found on the margin between the apices of 1A and Cu 2). In his figures of Hymenoptera, however (Ross 1936, figs. 3–5, 23), he shows Cu 1b turning abruptly caudad, crossing the claval furrow, where a bulla is formed, and meeting 1A proximad of the claval notch (Fig. 2). Because the vein called Cu 1b by Ross follows such a radically different course in Hymenoptera compared to that in the older orders, Megaloptera, etc., Ross's interpretation is questionable. Furthermore, if my interpretation of the distal section of Cu P in Hymenoptera is correct (see below), Ross's hypothesis calls for his Cu 1b to cross Cu P and meet 1A, a highly improbable course.

Another interpretation of "Cu 1b" in Hymenoptera is that it is a second cu-a crossvein. The Megaloptera (Ross 1936) and the extinct Miomoptera (Rasnitsyn 1980), groups postulated as possibly ancestral to Hymenoptera, are copiously supplied with crossveins. The second cu-a crossvein in Hymenoptera could well have a compound origin similar to that suggested for the first cu-a by Ross (1936, p. 106), i.e. crossveins extending from Cu A to Cu P and from Cu P to 1A lined up with one another during the reduction and loss of Cu P.

Modern thought (summarized in Wootton 1979) is that Cu P is closely associated with the claval furrow. In light of this it seems to me unreasonable to postulate that Cu A should have a branch crossing the site of Cu P (and the extant claval furrow) to join 1A. I think the existence of a second cu-a crossvein is a more tenable hypothesis for Hymenoptera. A truly branched Cubitus (Cu A1, Cu A2) can be seen in Stephanidae (Fig. 3).

Certainly Cu P existed in the forewing of many extinct Neopterous insects and is easily seen in extant forms, where it closely parallels the claval furrow. Ross (1936) drew attention to the trace (nebulous, Mason 1986) of a concave vein along the basal part of the claval furrow in forewings of Xyelidae and called it Cu 2 (Fig. 2), his equivalent of what recent authorities call Cu P. Significantly, there is a similar nebulous vein in Orussidae (Fig. 1). Recently (Mason 1986), I noticed a usually spectral concave vein in forewings of several groups of Apocrita, running distally from the junction of the claval furrow and 2nd cu-a (= Cu 1b, Ross). Further searching has revealed a concave spectral vein in phylogenetically old members of all apocritous major groups that have most of the venation preserved. At least some species of the following families have the vein present: Stephanidae, Megalyridae, Trigonalidae, Aulacidae, Monomachidae, Roproniidae, Ibaliidae, Cynipidae, Bethylidae, Scolebythidae, Tiphiidae, Sapygidae,



Figs. 3–10. Forewing of diverse Apocrita showing apical trace of Cu P branching from claval furrow. 3, *Schlettererius cinctipes* Cr. (Stephanidae); note 2 branches of Cu A. 4, *Monomachus* sp. (Monomachidae). 5, *Ropronia garmani* Ashm. (Roproniidae). 6, *Orthogonalys pulchella* Cr. (Trigonalidae); note minute jugum. 7, *Liosphex varius* Tow. (*Rhopalosomatidae*); note nebular Cu P, fusion of C and R, retention of lr and loss of stigma. 8, *Pristaulacus* sp. (Aulacidae); note jugum defined by convex wing fold. 9, *Pristocera atra* Klug (Bethylidae); note nebular adventitious vein (Ad.) between 1 cu-a and 2 cu-a, spectral concave combination of vein 2-M and medial furrow, concave spectral 2m-cu, c.v.-concave vein. 10, *Exeristes roborator* Grav. (Ichneumonidae); note nebular 1 − Rs + M, a unique feature for this family. (Conventions of delineation follow Mason (1986). Scale lines = 1 mm).

Anthoboscidae, Vespidae, Bradynobaenidae, Rhopalosomatidae, Astatidae, Hylaeidae, Ichneumonidae (Figs. 3–10). The Cu P vein is so widespread among primitive Apocrita that I suggest it to be a basic character of the Apocrita. The absence of the "vein" in Symphyta is puzzling. Either the distal part of Cu P disappeared completely in Symphyta and the vein in Apocrita is a newly evolved structure or Cu P is suppressed by some genetic mechanism in modern Symphyta. A poorly defined impression in some specimens of *Orussus* (Fig. 1) may be interpreted as Cu P and may hint that the suppressing mechanism was lost early in the evolution of Apocrita (perhaps among ancient Orussoidea?), thus allowing the vein to reappear (i.e. a reversal). Which choice one postulates is of little phylogenetic consequence; both mechanisms result in an apomorphy for Apocrita and the name to be used for the vein might as

well be Cu P in either case because its position and profile fit perfectly into a normal full venation.

Discussion

Ross (1936) uses elements of the two incompatible schemes; the Lameere nomenclature for branches of Media and the discredited Comstock scheme for branches of Cubitus. Therefore Ross's Cu 1 and Cu 2 should be now called Cu A and Cu P.

The vein Cu P is general in putative sistergroups of Hymenoptera and a basal relict is visible in some Symphyta (Xyelidae, Orussidae). An apical part of Cu P may be present as a trace vein in many generalized Apocrita but is absent in Symphyta with the possible exception of Orussidae. Its presence may be due to reversal of a character suppressed in Symphyta and is probably a synapomorphy for Apocrita.

The vein Ross called Cu 1b is probably not a branch of Cu A but most likely is a compound crossvein like the more proximal cu-a, composed of cua-cup and cup-a crossveins inherited from Permian or Triassic ancestors and aligned during the deterioration of Cu P.

My hypothesis is that some Hymenoptera have relicts of Cu P and that there are two cu-a crossveins.

I recommend the following modifications to the Ross system.

Ross 1936	Amendments
Cu	1st Cu A (1Cu)
Cu 1	2nd Cu A (2Cu)
Cu 1a	3rd Cu A (3Cu)
Cu 1b	2 cu-a
cu-a	1 cu-a
Cu 2 in Neoptera	Cu P

For sake of brevity vein Cu A in almost all Hymenoptera might as well be called Cu, just as the putative MA in Hymenoptera universally receives the appellation M. I suggest that the terms Cu A and Cu P could be retained only for forms that have both.

It is unfortunate that the final version of the logical and orderly system of Lameere (1922) (designating all concave veins with the prefix sub-) was never followed, but usage has now firmly fixed remnants of 3 different systems for naming 4 main concave veins: "Subcosta" (Redtenbacher 1886), the only concave vein that he named; "Radial Sector" (Comstock 1895), merely a convenience term to substitute for "R 2+3+4+5"; "Media Posterior" and "Cubitus Posterior" (Lameere 1922, and many earlier papers on the Commentry fossils, and Martynov 1924), 2 concave veins not recognized by Comstock. Other recently used names (empusal, plical) seem to be unnecessary innovations that probably add nothing to an understanding of phylogeny and needlessly complicate nomenclature (Wootton 1979). I agree with Wootton that conservation is a more sensible policy than the coining of new names. Specialists in Hymenoptera using other systems should not lose sight of the strength of Ross's system: the names of veins designate structures believed to be homologous throughout Insecta. Phylogenetic comparisons, even within Hymenoptera, are extremely difficult without such a universal system.

It is not surprising that the spectral distal part of Cu P should escape the notice of researchers dealing with Aculeata s. l. or Ichneumonidae for they rarely need to deal with spectral venation, but the vein is nebulous and plain to see in Rhopalosomatidae. Systems of nomenclature for venation used by most aculeate workers have presumably allowed the phylogenetic significance of a Cu P vein in Rhopalosomatidae to escape attention. Using a traditional naming system, Cu P would be called Brachius or some other term, and homology would be masked by the inadequacies of the traditional nomenclature system.

Literature Cited

Carpenter, F. M. 1966. The lower Permian insects of Kansas II. Psyche 73: 43–88.

Comstock, J. H. 1918. The Wings of Insects. Comstock, Ithaca, N.Y. 430 pp.

Comstock, J. H. *in* Comstock, J. H. and A. B. Comstock. 1895. A Manual for the Study of Insects. Comstock, Ithaca, N.Y. 701 pp.

Lameere, A. 1922. Sur la nervation alaire des insectes. Bul. Acad. Roy. Belg. (Cl. Sci.) 1922: 38–149.

Martynov, A. V. 1924. Sur l'interpretation de la nervuration et de la trachéation des ailes des Odonates et des Agnathes. Rev. Russe d'Ent. 18: 145–174.

Mason, W. R. M. 1986. Standard drawing conventions and definitions for venational and other features of wings of Hymenoptera. Proc. Ent. Soc. Wash. 88: 1–7.

Rasnitsyn, A. P. 1980. Proikhozhdenie i evolyutsiya pereponchatokrylykh nasekomykh. Trudy paleontologicheskovo instituta vol. 174, pp. 189 + 2.

Redtenbacher, J. 1886. Vergleichende Studien uber das Flugelgeader der Insecten. Ann. K.K. Hofmus. 1: 153–232.

Rohwer, S. A. and A. B. Gahan. 1916. Horismology of the hymenopterous wing. Proc. Ent. Soc. Wash. 18: 20–76.

Ross, H. H. 1936. The ancestry and wing venation of the Hymenoptera. Ann. Ent. Soc. Am. 29: 99–111.

Wootton, R. J. 1979. Function, homology and terminology in insect wings. Syst. Entomol. 4: 81–93.